Stability of Internal Heat Necrosis and Specific Gravity in Tetraploid × Diploid Potatoes

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ABSTRACT

Internal heat necrosis (IHN) is a severe physiological disorder of potato (*Solanum tuberosum* L.) tubers, characterized by brown spots that first appear near the apical end of the tuber parenchyma, although most of the parenchyma tissue is involved in severe cases. The purposes of this study were to evaluate 4x-2x clones of *S. tuberosum* × *S. phureja* Juz. & Bukasov–*S. stenotomum* Juz. & Bukasov (*phu-stn*) for specific gravity (SG) and incidence and severity of IHN in the mid-Atlantic states, and identify clones with low incidence and severity of IHN and high SG for future enhancement efforts in *S. tuberosum*. In 1999 and 2000, 26 and 88 4x-2x clones, respectively, and the check cultivar 'Atlantic' were grown in North Carolina, Virginia, and New Jersey, in a randomized complete block design with two replications. At harvest, tubers > 64 mm in diameter were rated for IHN. The SG was also determined. The correlation between incidence and severity of IHN was very high; however, there was no correlation between IHN and SG. There were significant differences among the clones for SG and IHN. There were also significant clone × location interactions for SG and IHN. Several 4x-2x clones were identified each year with significantly less IHN, and higher SG than Atlantic. The majority of these clones were stable both before and after removal of environmental heterogeneity. These results indicate that *phu-stn* has the potential to expand the tetraploid potato breeding base for both high SG and resistance to IHN in the mid-Atlantic states.

Potatoes are primarily a cool season crop, with the bulk of production in the USA harvested in the fall across the northern tier States. However, spring and summer potato production in the mid-Atlantic states was valued at $58 411 000 in 2000 (National Potato Council, 2001). Although this value is small in relation to the total value of potato production in the USA, the mid-Atlantic states produce ≈10% of the total spring production and >23% of the summer production in the country (National Potato Council, 2001). As a result of this spring and summer production, the 69 potato chip processing plants in the eastern USA have a fresh supply of product during this period.

Possessing the important traits of high yield, high SG, good chip color, and wide adaptability, Atlantic is the number one chipping cultivar grown in the USA (National Potato Council, 2001). However, Atlantic is susceptible to the physiological disorder IHN in which necrotic tissue develops within the pith of the tuber, rendering tubers unsaleable (Henninger et al., 1979; Sterrett and Henninger, 1997). In a 3-yr survey of North Carolina and Virginia growers, Sterrett and Wilson (1990) reported that 3.2 to 11.2% of the acreage of Atlantic was left unharvested when the tubers were off-grade because of IHN. The potential for economic loss exists in most spring and summer production areas where Atlantic is grown for chip processing directly from the field (S. Molnar, 2000, personal communication).

Symptoms of IHN in the tuber include round-to-irregular, light tan to reddish-brown spots or blotches occurring primarily in the parenchyma tissue internal to the vascular ring (Sterrett et al., 1991a). There are no external symptoms of IHN. Internal symptoms initially occur near the apical end of the tuber, but with time can spread to include most of the parenchyma tissue. A subjective scale developed by Sterrett and Henninger (1997) is used to document the severity of IHN.

Many other terms in the literature have been used to describe symptoms similar to those of IHN, including internal brown spot (Friedman, 1955), internal browning (Ellison and Jacob, 1952), internal physiological necrosis (Larson and Albert, 1945), chocolate spot (Kamal and Marroush, 1971), and internal rust spot (Seppanen, 1975; Collier et al., 1978).

The influence of several environmental factors on the expression of IHN has been studied. Iritani et al. (1984) reported that internal brown spot in 'Russet Burbank' was delayed with delayed planting date; a similar finding was reported by Sterrett et al. (1991b) for expression of IHN in round-white cultivars. Ellison and Jacob (1952) reported an increase in the incidence of internal brown spot with earlier planting dates in round-white cultivars. Delaying planting in the mid-Atlantic states reduces the marketable yield and economic return, thus limiting the potential of managing IHN by planting date (Sterrett and Henninger, 1997). Ellison and Jacob (1952) reported that tubers from plants with green vines had a greater incidence of IHN than those from dead vines. However, Sterrett and Henninger (1997) reported that in years where IHN was severe, vine-kill treatments did little to decrease the incidence of IHN over the non-vine-killed controls. With the associated reduction in yield, vine-killing did not offer an effective strategy for managing IHN in the mid-Atlantic states. Because IHN typically occurs in larger size tubers in current commercial cultivars, a more narrow in-row spacing is recommended to decrease the potential to develop oversized tubers (Sieczka and Thornton, 1993). However, increasing plant density is done at increased expense to the

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Abbreviations: DAP, days after planting; IHN, internal heat necrosis; *phu-stn*, *Solanum phureja–S. stenotomum*; SG, specific gravity.

producer. Minimum and maximum temperatures exceeding the optimum for potato growth, rainfall events, and tuber size distribution have been used in modeling to predict occurrence and development/severity of IHN in Atlantic in the mid-Atlantic states (Sterrett et al., 1991b).

High tuber SG is an important quality factor in the potato chipping industry. High-SG tubers yield more processed product per unit of raw product, and produce more rigid, crisp, and less oily chips (Kunkel et al., 1951). Little progress has been made in breeding for high SG since the release of Atlantic (Webb et al., 1978). Plaisted and Peterson (1963) reported that recurrent selection within the U.S. tetraploid potato germplasm base would not result in great increases in SG. They reported an average gain of ≈0.0004 in SG per selection cycle. Haynes et al. (1995) detailed the extensive use of 'Lenape', a high-SG potato and one of the parents of Atlantic, as an ancestor in many of the potato cultivars developed since Lenape (Akeley et al., 1968). Love et al. (1998) concur with this assessment and further state that the development of Lenape was responsible for a large portion of the progress that has been made in breeding for improved chipping quality since 1970. Atlantic and 'Snowden' are the two major high-SG potato cultivars widely grown in the USA (National Potato Council, 2001). These are half-sibs (Love, 1993), and both are susceptible to IHN.

Efforts are underway to breed new high-SG cultivars free of IHN for the mid-Atlantic region. Henninger et al. (2000) obtained high estimates of broad-sense heritability for IHN for several clones from the tetraploid USDA/ARS *S. tuberosum* germplasm breeding base when grown in the mid-Atlantic states. Although they found that there was generally no relationship between SG and susceptibility to IHN, they did report that clones derived from Atlantic were more susceptible to IHN. Thus, efforts to combine high SG and resistance to IHN in *S. tuberosum* alone have so far not been successful (Henninger et al., 2000).

One reason for the lack of improvement in SG may be the relatively narrow genetic base of *S. tuberosum* (Mendoza and Haynes, 1974). Alternate germplasm sources for the high-SG breeding effort have been developed using a diploid hybrid potato population of *phu-stn* (Haynes, 1972, 2001; Haynes and Haynes, 1990; Haynes et al., 1989, 1995; Ruttencutter et al., 1979). Many of the individual clones in this long-day adapted *phu-stn* population have significantly higher SG than Atlantic (Haynes, 2001). Moreover, about one-third of the total variation for SG in this population was reported to be additive genetic in nature (Haynes et al., 1989) and another one-third nonadditive genetic, with the remainder of the variation due to environment and genotype × environment interactions (Haynes et al., 1995). These findings are important considerations when utilizing this adapted population in 4x-2x crosses to enhance the tetraploid breeding base for alternate sources of high SG.

A large part of the genetic composition of a superior diploid clone can be sexually transmitted to its tetraploid progeny through first division restitution gametes (Peloquin, 1982). The actual amount of genetic variation transmitted sexually is a function of the mechanism of 2n pollen formation and the frequency of single exchange tetrads in the diploid parent (Haynes, 1990). The inbreeding coefficient of a 4x-2x hybrid is a complex function of the coancestry of the parents, the inbreeding of the parents, the coefficient of double reduction in the tetraploid parent, and the frequency of single exchange tetrads in the diploid parent, and depends on the mechanism of 2n pollen formation (Haynes, 1992; Haynes and Potts, 1993). Wannamaker and Collins (1992) reported that high SG could be transmitted to 4x-2x hybrids from high-SG diploid parents. To our knowledge, 4x-2x clones generated from this *phu-stn* population have not been evaluated for their resistance to IHN.

The purposes of this study were to: (i) evaluate several clones of 4x-2x *Solanum tuberosum* × *phu-stn* for incidence and severity of IHN and SG in the mid-Atlantic states; (ii) determine the stability of incidence and severity of IHN and SG in each clone; and (iii) identify clones with resistance to IHN and high SG for future enhancement efforts for these traits in *S. tuberosum*.

MATERIALS AND METHODS

Clonal Material

The 4x-2x clones evaluated in this study originated from controlled crosses made during the spring of 1991–1993 between advanced tetraploid *S. tuberosum* selections or cultivars and diploid *phu-stn* clones from the first selection cycle for high SG (Haynes, 2001), or from the yellow-flesh population that produced a high frequency of 2n pollen (Haynes, 2000). Seeds were extracted 6 to 8 wk after pollination, dried, and stored at 4°C and 40% relative humidity. True seed was allowed to age for at least 1 yr, then treated with 1500 mg kg^{-1} gibberellic acid for 24 h, rinsed with tap water, allowed to air dry, and sown in flats of Jiffy Mix (Jiffy Products of America, Inc., West Chicago, IL) during the fall of each year as they became available (1993–1995). These were subsequently transplanted into 8.9-cm clay pots filled with Jiffy Mix in the greenhouse at Beltsville, MD. In early December, the largest tuber from each pot was harvested, bulked by family, put into muslin bags, and placed in 4°C, 95% relative humidity storage. Tubers were shipped to Presque Isle, ME, in late April.

All clones were grown in the field following a plowed down timothy–clover (*Phleum pratense* L.–*Trifolium* spp.) sod cover crop with a soil pH ranging from 5.0 to 5.4. The test location was fertilized with 1200 kg ha^{-1} of 14-14-14 N-P-K banded in-row at planting. Cultural practices were similar to those used on commercial farms in the area.

In May of each year (1994–1996), seedling tubers were planted contiguously in the field on Chapman Farm, Presque Isle, ME, on a Caribou gravelly loam soil (fine-loamy, isotic, frigid Typic Haplorthods). At harvest, clones were selected on the basis of horticultural characteristics such as size, yield, relative smoothness, and nonsprouting for replanting the following year (1995–1997). These selections were replanted each of the next 2 yr and selected using the same criteria. Sufficient seed stock of 26 selections in the first group (from the 1994 and 1995 seedling generations) and 88 selections in the second group (from the 1996 seedling generation) was tested in the mid-Atlantic states (North Carolina, Virginia, New Jersey) in 1999 and 2000, respectively. Atlantic (highly susceptible to

IHN) and an advanced breeding selection, B9955-11 (highly resistant), were included as checks in 1999; only Atlantic was included in 2000.

In the year before testing in the mid-Atlantic states, five tubers from each of these clones were saved from the September harvest and evaluated (nonrandomized, nonreplicated evaluations) in Presque Isle, ME, for their chipping ability following storage at 10°C into December.

At each mid-Atlantic location, tubers were planted in a randomized complete block design consisting of two replicates of 20 hills per clone. Planting and harvest dates and soil type for each location are given in Table 1. At each location, all tubers were harvested from each plot, sized into groups < 48, 48 to 64, 64 to 83, and > 83 mm in diameter, and weighed. SG was determined from a sample of tubers 64 to 83 mm in diameter using the weight in air and weight in water method (Murphy and Goven, 1959). All tubers > 64 mm in diameter were counted, quartered longitudinally and scored for IHN using the subjective scale (1–9, where 1 = most of pith parenchyma tissue necrotic, 9 = no IHN) developed by Sterrett and Henninger (1997).

Statistical Analysis

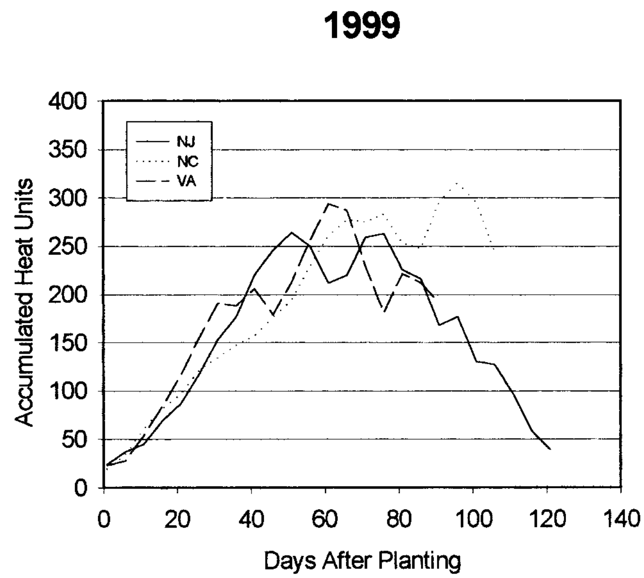
Two IHN variables for each plot were calculated. Incidence of IHN was calculated as the number of tubers showing symptoms of IHN and divided by the total number of tubers. Severity of IHN was calculated for all tubers > 64 mm in diameter by multiplying the number of tubers within each category by the score for that category summed across all categories and divided by the total number of tubers. The correlations among incidence and severity of IHN and SG were calculated for each environment. Incidence and severity of IHN and SG were analyzed for all 4x-2x clones and the check cultivars, using the mixed procedure in the Statistical Analysis System (Littel et al., 1996), considering locations, clones, and the location × clone interaction to be fixed. Error variability was partitioned to accurately model the differently-sized variation among locations. For significant clone × location effects, appropriate contrast statements were used to compare incidence and severity of IHN, and SG between Atlantic and the other clones within a location, with the exception that Atlantic was not evaluated for IHN in North Carolina in 2000. Least square means (clonal marginal means) for the 4x-2x clones by location were computed for incidence and severity of IHN, and SG, and the clone × location interaction was partitioned into stability-variance components (σ_i^2) assignable to each clone (Shukla, 1972), using the interactive matrix language procedure in SAS (Kang, 1989). An environmental index was calculated for each variable as the least square mean of all clones across all three locations minus the least square mean of all clones in each location. Heterogeneity, or nonadditivity, due to this environmental index was removed from the clone × location interaction, and the remainder of the clone × location interaction was partitioned into s_i^2 components assignable to each clone (Kang, 1989).

Table 1. Planting and harvest dates for the 26 and 88 4x-2x potato clones evaluated in the internal heat necrosis study conducted in Bridgeton, NJ, Painter, VA, and Plymouth, NC, in 1999 and 2000, respectively.

Location	Year	Planting Date	Harvest Date	Days to Harvest
Plymouth, NC	1999	17 March	8 July	112
Painter, VA	1999	22 April	26 July	94
Bridgeton, NJ	1999	6 April	10 August	125
Plymouth, NC	2000	14 March	11 July	118
Painter, VA	2000	8 March	11 July	124
Bridgeton, NJ	2000	7 April	7 August	121

RESULTS AND DISCUSSION

Differences in temperature stress between years and locations can be seen using the accumulated heat unit model developed by Lee et al. (1992) (Fig. 1). In this model, heat stress results in a reduction in accumulated heat units since a penalty is imposed when the temperature exceeds the optimum maximum or minimum. The steeper slope of the accumulated heat units plotted on days after planting (DAP) for New Jersey and Virginia in 1999 suggest temperatures consistently approaching the maximum and minimum optimum for potato (25° and 21°C, respectively). Slower accumulation of heat units early (0–60 DAP) and greater total accumulated



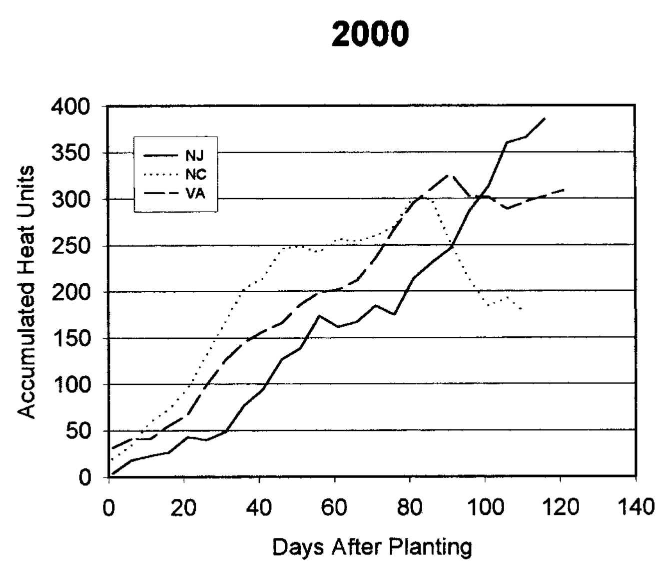


Fig. 1. Accumulated heat units according to the model of Lee et al. (1992) during the growing season for Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 1999 and 2000.

Table 2. Correlations among incidence and severity of internal heat necrosis and specific gravity for 4x-2x clones grown in Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 1999 and 2000.

		Incidence		Specific Gravity	
	Location	1999	2000	1999	2000
Severity	North Carolina	−0.89**	−0.89**	−0.07	0.08
	Virginia	−0.94**	−0.91**	−0.10	0.05
	New Jersey	−0.88**	−0.95**	−0.03	−0.02
Specific Gravity	North Carolina	−0.08	−0.11	–	–
	Virginia	0.02	−0.04	–	–
	New Jersey	−0.04	0.00	–	–

** Significant at the 0.01 level of probability.

heat units is indicative of cooler growing conditions for New Jersey and Virginia than North Carolina in 2000.

The correlations between incidence and severity of IHN at all locations in 1999 ($-0.88 < r < -0.94$) and 2000 ($-0.89 < r < -0.95$) were very strong (Table 2). There was no correlation between either incidence or severity of IHN and SG (Table 2).

There were no significant differences for incidence or severity of IHN among locations in 1999 (Table 3). Because of the high correlations between incidence and severity, and space limitations, only specific data for incidence of IHN will be reported further, although severity of IHN will be discussed in general terms. The mean incidence and severity of IHN for all clones in 1999 was 0.23 and 8.39, respectively. However, there were significant differences among locations for incidence and severity of IHN in 2000 (Table 3). Incidence and severity of IHN ranged from 0.42 and 7.72 in Virginia to 0.19 and 8.42 in New Jersey, respectively; North Carolina was intermediate at 0.30 and 8.06, respectively.

There were significant differences for incidence and severity of IHN among 4x-2x clones in 1999 and 2000 (Table 3). The mean incidence of IHN in Atlantic was 0.63 in 1999 (Fig. 2) and 0.37 in 2000 (Fig. 3). The mean severity of IHN in Atlantic was 7.50 and 8.01 in 1999 and 2000, respectively. In 1999, the average incidence of IHN for the 26 4x-2x hybrids ranged from 0.00 to 0.86 (Fig. 2) and severity ranged from 5.45 to 9.00. In 2000, the average incidence for the 88 4x-2x hybrids ranged from 0.00 to 0.92 (Fig. 3) and severity ranged from 3.15 to 9.00. Among the 1999 4x-2x hybrids, 17 of 26 had significantly less IHN than Atlantic at all three locations; all but four of these were stable before removal of environmental heterogeneity and only one was unstable after removal of environmental heterogeneity. Of those tested in 2000, 69 of 88 4x-2x hybrids had equal

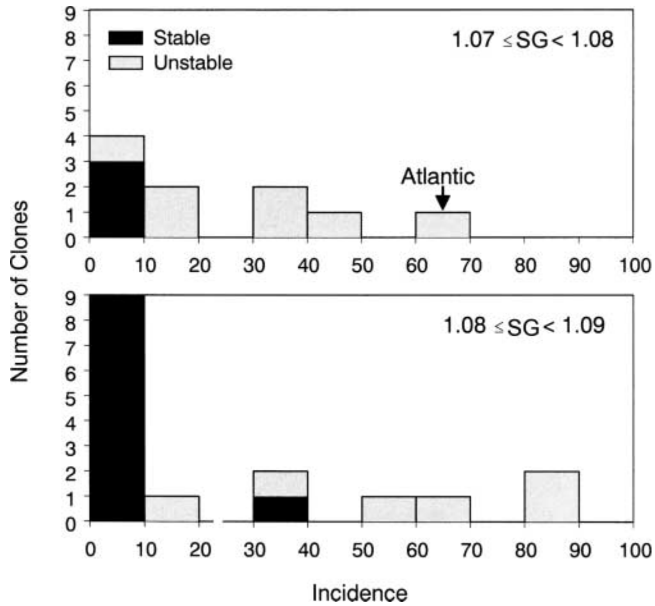


Fig. 2. Distribution of clones for incidence (× 100) of internal heat necrosis and stability before (σ_i^2) removal of environmental heterogeneity and specific gravity (SG) for the 26 4x-2x clones and the two checks ('Atlantic' and B9955-11) grown in Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 1999. Two clones with SG > 1.090 are not shown.

or significantly less IHN than Atlantic at either of the two locations where Atlantic was evaluated; however, none had significantly less IHN at both locations. No clones had significantly less IHN than Atlantic in Virginia. Although the mean incidence of IHN was similar at both locations (0.36 vs. 0.37), the much greater variability in Virginia compared with New Jersey (σ_e^2 = 0.26 vs. 0.009) made it impossible to show that clones without IHN had significantly less IHN than Atlantic (incidence = 0.36). Twenty-two clones were unstable for incidence of IHN before (Fig. 3) and after environmental heterogeneity was removed.

There were significant differences among locations for SG in 1999 (Table 3). In general, SG increases the further north potatoes are grown. However, in 1999, the highest SG in this study was observed in North Carolina. There were relatively few penalty days (days when the maximum and/or minimum temperatures exceeded the optimal for potato development) associated with the accumulated heat unit model of Lee et al. (1992) in North Carolina, whereas, as evidenced by the rapid decline in accumulated heat units in Virginia and

Table 3. Tests of fixed effects from the analysis of variance on incidence and severity of IHN and specific gravity (SG) for 26 and 88 4x-2x clones plus check clones grown in Bridgeton, NJ, Painter, VA, and Plymouth, NC, in 1999 and 2000, respectively.

	1999					2000				
Source	NDF†	DDF‡	Incidence	Severity	SG	NDF	DDF	Incidence	Severity	SG
location	2	3	ns§	ns	**	2	3	**	**	**
clone	27	81	**	**	**	88	262	**	**	**
clone × location	54	81	**	**	**	176	262	**	**	**

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
† NDF = numerator degrees of freedom.
‡ DDF = denominator degrees of freedom.
§ ns = not significant.

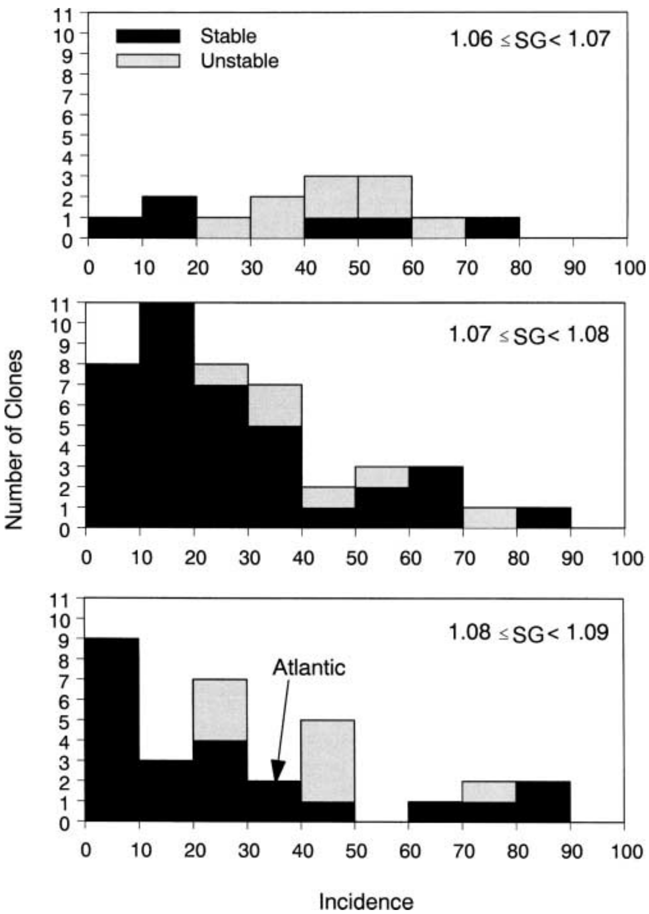


Fig. 3. Distribution of clones for incidence (× 100) of internal heat necrosis and stability before (σ_i^2) removal of environmental heterogeneity and specific gravity (SG) for the 88 4x-2x clones and the check ('Atlantic') grown in Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 2000.

especially New Jersey, conditions were more stressful late in the growing season (Fig. 1). In 2000, the SG ranged from 1.069 in North Carolina to 1.082 in New Jersey and followed the generally accepted pattern of increasing SG from southern to northern locations. The potatoes grown in North Carolina were under the most heat stress, as evidenced by the steep decline in accumulated heat units late in the growing season; potatoes in Virginia were under more moderate stress and those grown in New Jersey were under the least stress of the three locations (Fig. 1).

There were also significant differences for SG among clones in 1999 and 2000 (Table 3). The mean SG of Atlantic was 1.076 and 1.081 in 1999 and 2000, respectively. The mean SG of the 4x-2x clones grown in 1999 ranged from 1.071 to 1.097 (Fig. 2) (two clones with SG $>$ 1.090 not included in figure). Of these, the SG of all but one clone were equal to or greater than that of Atlantic. Only three 4x-2x clones were unstable before the removal of environmental heterogeneity and two were still unstable after the removal of environmental heterogeneity. In 2000, 49 of the 88 4x-2x clones had a SG greater than or equal to the SG of Atlantic at all three locations. Only 14 4x-2x clones were unstable for SG before environmental heterogeneity was removed; nine were unstable after environmental heterogeneity was removed.

In the year before their evaluation for IHN in the mid-Atlantic states, tubers from these 4x-2x hybrids were processed into potato chips out of 10°C storage into December in Presque Isle, ME. In the first group, all but two of the clones chipped acceptably; and in the second group, 66 of the 88 4x-2x clones processed as well as Atlantic. There were neither time nor facilities to process tubers into chips from these clones in the mid-Atlantic states, but generally, clones which process from early storage in Maine will process directly from the field in the mid-Atlantic states. Many of these clones produced chips much lighter in color than Atlantic (data not shown).

The diploid parents involved in the 4x-2x crosses reported herein were from the same population of clones that Haynes et al. (1995) reported to be stable for SG both before and after removal of environmental heterogeneity. This group of diploid clones has thus successfully transmitted not only high SG to their tetraploid progeny, but stable high SG.

These data suggest that the introduction of this diploid hybrid *phu-stn* germplasm into the tetraploid breeding base has significantly improved the population for resistance to IHN and added new genetic material for high SG. Many of the 4x-2x hybrids generated and evaluated in this study have combined both high SG and resistance to IHN, a combination of characteristics currently unavailable in commercial potato cultivars (Fig. 2 and 3, Table 4). Nondormancy is a characteristic of *S. phureja*, whereas longer dormancy is a characteristic of *S. stenotomum*. The original diploid *phu-stn* population from which these 4x-2x hybrids were generated has been selected against sprouting at harvest for 11 cycles of selection. In the initial selection cycles in Presque Isle, ME, 4x-2x clones were saved which were also not sprouting at harvest. Many of these 4x-2x hybrids have a shorter dormancy period than commercial *S. tuberosum*. This should not be a problem in using this material to develop new cultivars for the chipping industry in the mid-Atlantic states, since these areas plant so much earlier than the northern tier states. Shorter dormancy would actually be beneficial to areas such as North Carolina, which are planting as early as late February or early March, and Virginia and New Jersey, which are planting as early as March or April and which buy their seed from the late-harvesting (September and October) northern tier states. Shorter dormancy should also not pose much of a problem following harvest in these mid-Atlantic areas, as most of the potatoes are used in the processing industry within three days of harvest in the mid-Atlantic states. No sprouting was observed in this material for up to the 2 wk it took to collect all the data following each harvest.

The underlying physiological and/or biochemical mechanisms for resistance to IHN is currently unknown. The possible role of Ca on internal disorders has been discussed by Olsen et al. (1996). Calcium is important in maintaining cell wall stability and integrity (Iiyama et al., 1994). Tubers have low levels of endogenous Ca

Table 4. Incidence of internal heat necrosis (IHN) and specific gravity and stability-variance statistics before (σ_i^2) and after (s_i^2) the removal of environmental heterogeneity for a few of the most resistant and most susceptible 4x-2x clones grown in Plymouth, NC, Painter, VA, and Bridgeton, NJ, in 2000.

Clone	Incidence of IHN†					Specific Gravity‡				
	NC	VA	NJ	σ_i^2	s_i^2	NC	VA	NJ	σ_i^2	s_i^2
'Atlantic'	NT	0.36	0.37	–	–	1.073	1.084	1.087	–	–
BTD0105-2	0.98	0.88b	0.78b	ns§	ns	1.071	1.086	1.094	*	ns
BTD0111-1	0.00	0.03	0.00a	ns	ns	1.072	1.074b	1.080	ns	ns
BTD0112-3	0.00	0.00	0.03a	ns	ns	1.076	1.084	1.087	ns	ns
BTD0114-1	0.30	0.16	0.50	**	ns	1.056b	1.065b	1.068b	ns	ns
BTD0118-5	0.13	0.28	0.03a	ns	ns	1.077	1.072b	1.077b	**	ns
BTD0120-2	0.55	0.68	0.29	ns	ns	1.069	1.078	1.079b	ns	ns
BTD0124-5	0.19	0.14	0.00a	ns	ns	1.057	1.070b	1.066b	ns	*
BTD0127-3	0.73	0.92b	0.78b	ns	ns	1.065	1.079	1.081	ns	ns
BTD0128-5	0.20	0.60	0.25	ns	ns	1.060b	1.075b	1.081	ns	ns
BTD0135-1	0.13	0.05	0.05a	ns	ns	1.078	1.080	1.088	ns	ns
Mean of all 88 4x-2x hybrids	0.29	0.42	0.19			1.069	1.077	1.082		

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
† Within a location, means followed by an 'a' have significantly less incidence of IHN than 'Atlantic' at the 5% level; means followed by a 'b' have significantly higher incidence of IHN than Atlantic at the 5% level.
‡ Within a location, means followed by an 'a' have significantly higher specific gravity than Atlantic at the 5% level; means followed by a 'b' have significantly lower specific gravity than Atlantic at the 5% level.
§ ns = not significant.

(Wiersum, 1966; Davies and Millard, 1985). The uptake of Ca by potato plants and its distribution within the plant can be affected by high temperatures (Wiersum, 1979). With high transpiration rates, more Ca is transported to the vegetative portions of the plant and less to the tubers (Silva et al., 1991). Research by Bamberg et al. (1993) suggests that there is variation within *Solanum* germplasm for the ability to accumulate Ca. They found that the accessions of *S. stenotomum* tested were as poor as *S. tuberosum* in their ability to accumulate Ca. Unfortunately, their study did not examine the ability of *S. phureja* to accumulate Ca. Research is currently underway to determine the ability of some of these 4x-2x clones to accumulate Ca, particularly the ones listed in Table 4 representing some of the most resistant or susceptible IHN clones.

With the wide variation in responses to both IHN and SG that exists in this 4x-2x population, selected individual clones can now be investigated to determine a possible mode of action for resistance to this physiological disorder, and associate this trait with molecular markers.

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